

BIRD COMMUNITIES IN NATURAL FOREST PATCHES IN SOUTHERN BRAZIL

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ABSTRACT.—Avifaunal composition was evaluated for natural (not artificial) patches of mixed temperate rain forest in the Campos Gerais region, Paraná State, southern Brazil. A large patch (840 ha) and 11 smaller patches (0.5–40 ha) were censused from September to December of 1995 (five hours per month, each site). The total species number was strongly correlated with patch size ($r = 0.92$, $P < 0.001$). However, the number of edge species increased with decreasing patch area; the opposite happened with forest species. Thus, the ratio of edge to forest species increased with decreasing patch area. The number of leaf insectivore species decreased the most with a decrease in area. The mean Simpson similarity index was 73.8% among forest patches of similar size. Smaller forest patches linked to the 840 ha patch were more similar to this larger patch than isolated patches. Point counts from January to December 1991 in four patches (72 points each area) showed that several species, specially trunk (and twig) insectivores and omnivores, increased in relative abundance with decreases in area of the patch (density compensation). The “habitat appropriation” hypothesis, the expansion of niches to include slightly different habitats, could explain the increased relative abundance of two trunk (and twig) insectivores: *Craniolenca obsoleta* and *Craniolenca pallida*. Received 15 Oct. 1998, accepted 19 Feb. 1999.

Forest fragmentation in the Neotropical region has been considered an important force in the loss of biodiversity (Bierregaard and Lovejoy 1989). Decreases in the number of bird species and changing avifaunal composition have been documented by many workers (Willis 1974, 1979; Karr 1982; Bierregaard 1990; Anjos 1992; Aleixo and Vielliard 1995).

Density compensation (increased relative abundance of species in biologically isolated habitats) is another frequent feature in habitat fragments (MacArthur et al. 1972, Wright 1980). Reduced competition, habitat differences, and differences in colonization (Ricklefs and Cox 1978, Blondel 1991) also have been suggested as possible reasons for density compensation in habitat fragments. Blondel and coworkers (1988) presented the “habitat appropriation” hypothesis in which populations increase on islands because of expansion into additional habitats.

Studies of birds in Neotropical forest fragments have been carried out after fragmentation took place through logging. The state of Paraná, southern Brazil, has a grassland re-

gion called “Campos Gerais” with isolated forest patches of 0.1–100 ha (Fig. 1). This landscape is natural; it was not deforested by humans. The forest patches appear in areas of suitable soil conditions surrounded by grassland and are slowly increasing in area through a natural ecological succession (Klein 1960, 1972). The forest structure among different patch series is similar (Klein 1960, Maack 1981, Klein and Hatschbach 1971). Because fragmentation has been natural, the biological processes may not have been affected by human activity. Our goal in this study was to analyze the differences in the composition of the bird community among various-sized forest patches in Campos Gerais region.

STUDY AREA AND METHODS

Study sites.—The study areas are the Fazenda Santa Rita (25° 15' S, 49° 48' W) and Vila Velha State Park (25° 15' S, 49° 55' W), Paraná State, southern Brazil, in a region called Campos Gerais (Fig. 2). The patches of forest are mixed temperate rainforest. The dominant trees are: *Araucaria angustifolia* (Araucariaceae), *Podocarpus lambertii* (Podocarpaceae), *Sebastiania comersoniana* (Euphorbiaceae), *Ocotea porosa*, and *Nectandra grandiflora* (both Lauraceae; Klein and Hatschbach 1971). The average annual temperature is 17.3° C, varying from 20.9° C during summer (December–February) and 14.1° C during winter (June–August). The range of average annual precipitation is 1500–2000 mm. Elevations range from 950–1100 m a.s.l. (Maack 1981).

Eleven forest patches (called B, C, D, E, F, G, H, I, J, L and M) from 0.5–40 ha in size and one large forest patch of 840 ha (called A) were censused. All these

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FIG. 1. Landscape in the "Campos Gerais" region, southern Brazil; grassland with naturally isolated forest patches.

sites are covered by similar forest structure. Some patches are linked (patches B, C, D, and E) to the largest forest patch (A) by forest corridors while others are completely isolated by grassland (Table 1).

Species composition.—Bird species in each patch, micro-habitat, and feeding habit were recorded during five-hour monthly visits in the morning (20 h total) September–December, 1995. Each species was classified as to its typical habitat and feeding habit through field observations and references (Fitzpatrick 1980; Belton 1984, 1985; Sick 1997; Ridgely and Tudor 1989, 1994). The habitats were categorized as open area, forest border (up to 5 m from the edge), and forest interior. We divided the forest into three levels: (1) understory (below 2 m), (2) mid-levels (2–7 m) and (3) canopy (above 7 m). Feeding habits were categorized as: omnivore, insectivore, frugivore, carnivore or nectarivore. For insectivores, the area where the insect or its larvae was most often captured was also recorded. Three classes of capture sites were defined: (1) trunk (and twigs), (2) leaves, and (3) generalized insectivores.

Relative abundance.—Relative abundance was determined by monthly point counts of unlimited distance (Blondel et al. 1970) January–December in 1991. Fifty-three points were used to calculate relative abundance: 24 in A, 12 in B, 10 in C, and 7 in G. Each point was 100 m from another and at least 50 m from the edge of the forest. Each month six points in each site were chosen at random to be sampled giving

a total of 72 counts per site during the year (288 point counts total in the four sites). The relative abundance of each species was determined by dividing the total number of species contacts by the total number of points (72) sampled in each patch (Blondel et al. 1970). Sampling began at dawn at the first randomly selected point and finished about 3.5 h later at the sixth point. The time for sampling at each point was 20 min. Species were identified primarily by sound (99%). The same observer (LdA) performed all counts. Each pair or flock of each species was counted once (one contact) while vocalizing. Precautions were taken not to count the same individual or group more than once (a form was used in order to locate the counted individuals), especially highly mobile species. Bird recordings (1601 recordings of 414 species, deposited in the Bioacoustic Laboratory of the Universidade Estadual de Londrina) were used to aid identification. The observer had six years (1984–1990) of field experience in species identification in the region (Anjos 1992, Anjos and Graf 1993, Anjos et al. 1997).

Analyses.—The birds were identified mostly using the taxonomy of Meyer de Schauensee (1982) and Sick (1997). Similarities in bird species composition between forest patches were determined using the Simpson Index. β diversity (Whittaker 1960) was used to measure the degree of turnover in species composition along the six points sampled monthly (in A and G). This index is a measure of how different the samples were, in terms of the variety of species. Differ-

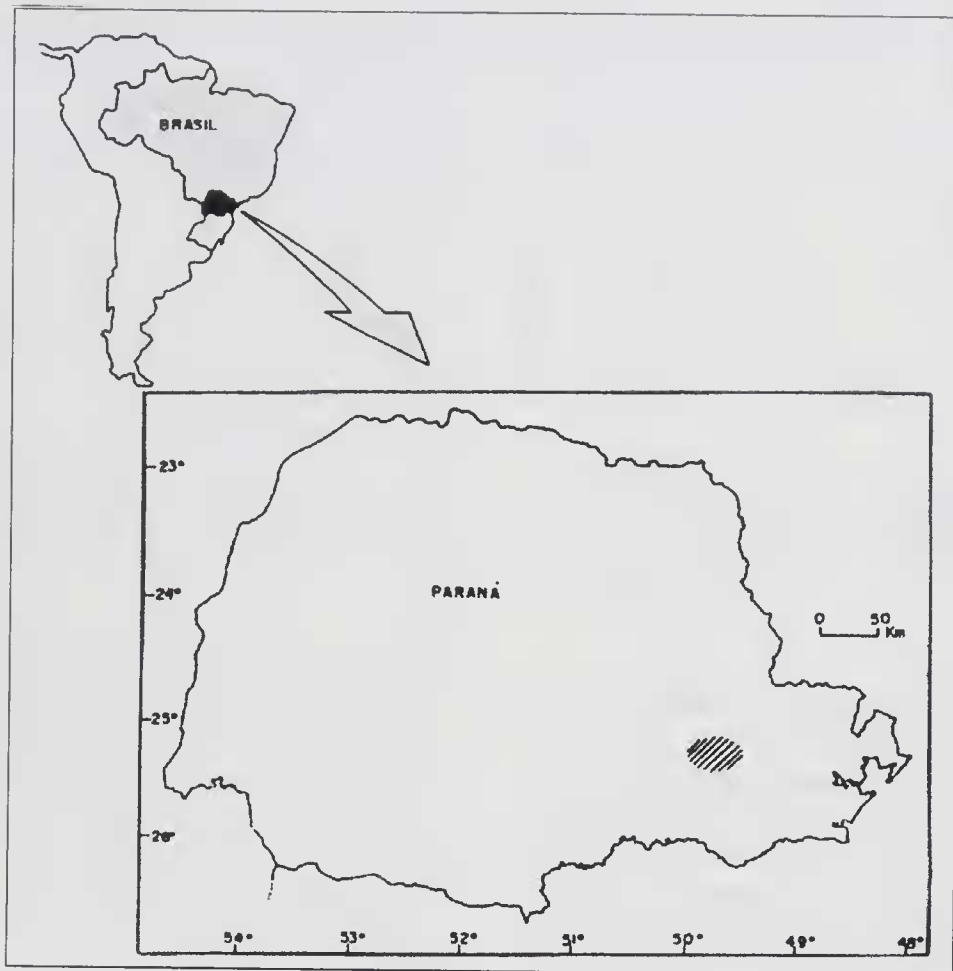


FIG. 2. Study area in "Campos Gerais" region, Paraná State, southern Brazil, indicated by hatching.

ences in numbers of species or numbers of contacts of species between the sites were tested with χ^2 analysis at $\alpha < 0.05$. Analysis of Variance (one way ANOVA) and the Tukey multiple range test ($P < 0.05$) were used to evaluate the average number of species and contacts recorded per sampled point in A, B, C and G. The relationship between number of bird species and size of fragment was expressed through a transformation following Preston (1962): $\log S = \log k + z \log A$ where

S is the number of species and A is the size of the area. SAS/STAT (version 6.11, IBM, mainframe) was used to calculate most of the above values.

RESULTS

Habitat distribution.—Birds in all patches totaled 189 species, including 13 open area species, 51 edge species, and 125 forest species (Appendix). The open area birds used the forest only for roosting and/or for nesting but not for foraging.

There were 13 edge species in the largest patch (A) and 32 species in the 6.5 ha fragment (I). By contrast, there were 93 forest species in the largest patch and only 13 species in the smallest fragment (M; Table 2). These results indicate a general decrease in the ratio of forest to edge species with a decrease in area (Fig. 3). The exceptions are the patches E (34/21 species), G (41/28 species), and L (32/19 species). The number of understory forest species decreased faster ($\chi^2 = 15.37$, $df = 2$, $P < 0.05$) with decrease in area of forest (33 species in A, 20 species in B, and 8 spe-

TABLE 1. Size (ha) and on the distance (m) from a continuous forest of each study site.

Site	Size	Type-Distance
A	840 ha	continuous forest
B	40 ha	linked by forest corridor-100 m
C	20 ha	linked by forest corridor-200 m
D	12 ha	linked by forest corridor-600 m
E	10.5 ha	linked by forest corridor-400 m
F	10 ha	isolated-3000 m
G	9 ha	isolated-2000 m
H	8.5 ha	isolated-800 m
I	6.5 ha	isolated-2500 m
J	4 ha	isolated-1500 m
L	1.5 ha	isolated-500 m
M	0.5 ha	isolated-1000 m

TABLE 2. Number of bird species in the study sites according their habitats and feeding habits.

	Sites											
	A	B	C	D	E	F	G	H	I	J	L	M
Habitats												
Open area	2	2	3	3	6	2	4	4	3	3	1	1
Edge	13	22	26	29	21	27	28	29	32	30	19	30
Forest/understory	33	20	8	10	5	8	8	4	10	4	7	3
Forest/mid-levels	32	29	27	22	20	17	23	18	16	15	17	6
Forest/canopy	28	19	16	12	9	5	10	7	7	7	8	4
Feeding Habits												
Omnivores	29	32	28	31	22	19	27	28	23	24	21	16
Insectivores/trunk	18	14	12	10	10	7	10	6	3	4	6	3
Insectivores/leaves	30	16	16	13	9	11	15	10	11	10	8	7
Insectivores/general	11	12	8	10	9	12	12	7	16	10	8	11
Frugivores	15	12	12	7	8	6	5	6	8	8	8	5
Carnivores	3	3	2	4	3	3	3	4	4	2	1	1
Neotariivores	2	3	2	1	0	1	1	1	3	1	0	2
Total Species	108	92	80	76	61	59	73	62	68	59	52	45

cies in C) than mid-level forest species (32 species in A, 29 species in B, and 27 species in C; $\chi^2 = 0.43$, $df = 2$, $P > 0.05$); canopy forest species were intermediate in the ratio of decreasing (28 species in A, 19 species in B, and 16 species in C; $\chi^2 = 3.71$, $df = 2$, $P > 0.05$; Table 2).

Similarity between sites.—The similarity index (Simpson) between the largest site (A: 108 species) and the smallest (M: 45 species) was 40% (17 species common to both sites); however, the mean was $73.8 \pm 2.7\%$ (SE) among forest patches of similar size.

The number of species was correlated with area (Fig. 4; $r = 0.92$, $df = 10$, $P < 0.001$). Species living in open areas were not consid-

ered in this analysis; edge species were included with forest species because the majority of them were commonly found within the forest. The number of species can be predicted according to the Preston (1962) model: $\log S = 3.81 + 0.17 \log A$, where S is the number of species and A is the fragmented area in ha.

Feeding habits.—Of the 189 species recorded, 85 were insectivores, 58 omnivores, 28 frugivores, 12 carnivores, and 6 nectarivores. Among the insectivores, 33 were leaf insectivores, 31 generalized insectivores (capture insects in various ways), and 21 trunk insectivores.

Insectivores were less abundant in B (40 ha;

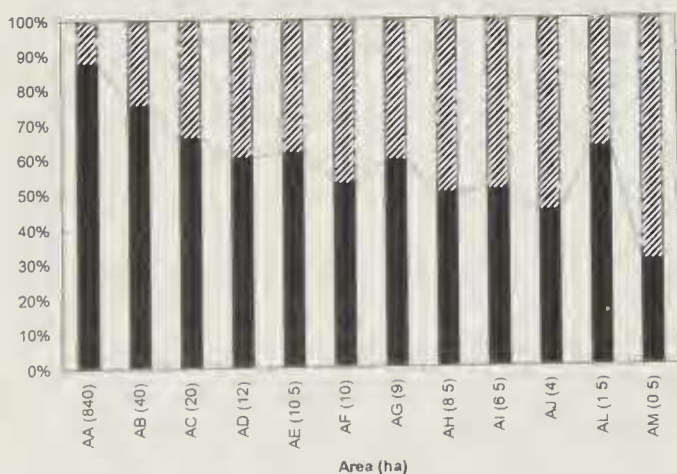


FIG. 3. Ratio of forest (solid) and edge (hatched) species in the study sites. Sites B–E linked to A by forest corridors.

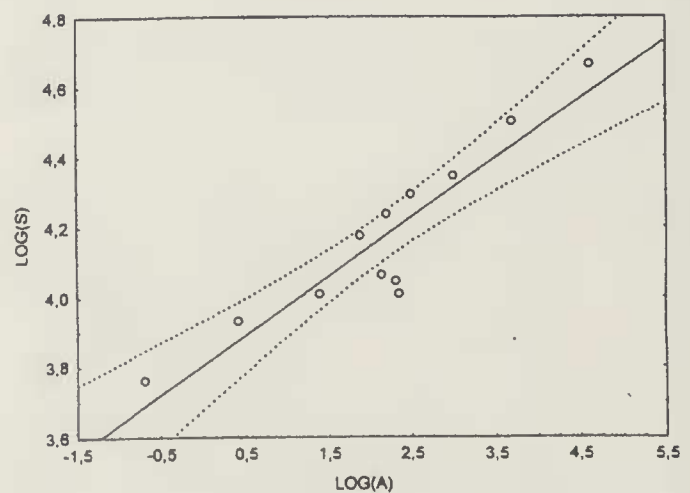


FIG. 4. Correlation (log/log) between number of species (S) and area (A) of fragment. Dotted lines indicate 95% confidence interval.

42 species) than in A (840 ha; 59 species) although not significantly so ($\chi^2 = 2.86$, $df = 1$, $P > 0.05$). In patches smaller than 40 ha the rate of decrease slowed as patch size diminished (36 species/20 ha, 33 species/12 ha, 28 species/10.5 ha); in patches smaller than 10.5 ha, there was no clear pattern (Table 2). The greatest reduction in species occurred in leaf insectivores, from 30 species in the forest (A) to 16 species in the largest patch (B; $\chi^2 = 4.26$, $df = 1$, $P < 0.05$); the loss of trunk insectivores was not so great (18 species in A and 14 species in B; $\chi^2 = 0.5$, $df = 1$, $P > 0.05$) while generalized insectivores gained one species (11 species in A and 12 species in B).

Omnivores were represented by two more species in B (32 species) than in A (30 species). Their numbers remained relatively constant down through the 12 ha patch (D; 31 species) but decreased in smaller patches (Table 2).

Frugivores decreased slightly in number ($\chi^2 = 0.46$, $df = 2$, $P < 0.05$) from A (15 species) to B and C (both with 12 species). The number of frugivores stayed between 5 and 8 species in patches smaller than 12 ha (Table 2).

Carnivores and nectarivores were represented by few species in all sites (1–4 species; Table 2).

Number of species and contacts.—In point counts conducted in 1991 we recorded 138 species in A, 125 in B, 103 in C, and 91 in G. The average numbers of species per sampled point were: 23.6 in A, 16.5 in B, 18.5 in C, and 21.4 in G. The number of species per sampled point was not significantly different (Tukey test: $P > 0.05$) between A and G although they are different in the size and total number of species recorded. The intermediate-sized patches B (40 ha) and C (20 ha) did not show significant differences (Tukey test: $P > 0.05$) among the numbers of species per sampled point, but both were significantly different from A and G (Tukey test: $P < 0.05$).

The average numbers of contacts per sampled point were: 27.0 in A, 19.1 in B, 22.1 in C, and 25.8 in G. The numbers of contacts per point were not significantly different between A and G nor between B and C; but they were significantly different between A–B, A–C, G–B and G–C (Tukey test: $P < 0.05$).

There were variations in the average num-

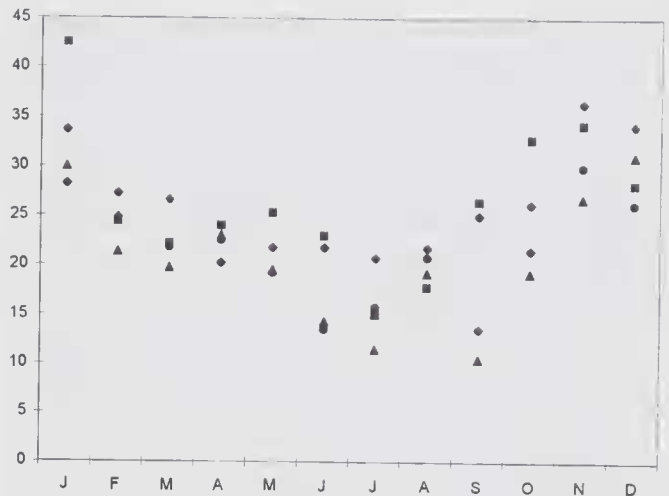


FIG. 5. Average number of contacts in the studied sites during the year. Square = A, triangle = B, circle = C, diamond = G.

ber of contacts during the year in the four study sites. The number of contacts was highest in September/October–January than February–August (Fig. 5).

Relative abundance.—The highest relative abundance (number of contacts divided by the number of sampled points) in this study was *Basileuterus leucoblepharus* (1.2) followed by *Turdus rufiventris* (0.85), *Lepidocolaptes squamatus* (0.68), *Basileuterus culicivorus* (0.68), *Cyclarhis gujanensis* (0.67), and *Cranioleuca obsoleta* (0.61).

The majority of species recorded in the point counts presented significant differences in the values of relative abundance when occurring in three or four sampled sites (indicated with “s” in Appendix; $df = 2$ or 3 , $P < 0.05$). Some of these species increased in abundance with the decrease in area (density compensation) such as *Veniliornis spilogaster*, *Cranioleuca obsoleta*, *Turdus amaurochalinus*, *Cyclarhis gujanensis*, *Parula pitayuni*, *Thraupis sayaca*, and *Stephanophorus diadematus*. The distribution of the abundances in a rank order showed that the 12 species with highest abundances (indicated with an * in Appendix) in the smallest patch analyzed (G) comprised 27% of total contacts but they comprised only 20% in the continuous forest (A).

Relative abundance increased with decreasing area for 12 omnivorous species (Appendix): *Penelope obscura* ($\chi^2 = 9.12$, $df = 3$, $P < 0.05$), *Pachyramphus polychopterus* ($\chi^2 = 73.87$, $df = 3$, $P < 0.001$), *Pitangus sulphuratus* ($\chi^2 = 106.39$, $df = 3$, $P < 0.001$), *Elaen-*

ia mesoleuca ($\chi^2 = 23.38$, $df = 3$, $P < 0.001$), *Cyanocorax caeruleus* ($\chi^2 = 21.08$, $df = 3$, $P < 0.001$), *Turdus rufiventris* ($\chi^2 = 8.52$, $df = 3$, $P < 0.05$), *Turdus amaurochalinus* ($\chi^2 = 23.9$, $df = 3$, $P < 0.001$), *Cyclarhis gujanensis* ($\chi^2 = 36.19$, $df = 3$, $P < 0.001$), *Stephanophorus diadematus* ($\chi^2 = 12.92$, $df = 3$, $P < 0.01$), *Thraupis sayaca* ($\chi^2 = 19.8$, $df = 3$, $P < 0.001$), *Zonotrichia capensis* ($\chi^2 = 33.64$, $df = 3$, $P < 0.001$), and *Carduelis magellanicus* ($\chi^2 = 14.07$, $df = 3$, $P < 0.01$). The sum of relative abundances of the omnivorous species increased ($\chi^2 = 28.41$, $df = 2$, $P < 0.001$) from A (6.56) to the patches C (7.52) and G (9.0).

The sum of relative abundances of leaf insectivorous species was highest ($\chi^2 = 77.15$, $df = 3$, $P < 0.001$) in A (8.42), followed by G (6.18), C (5.56), and B (5.14). *Parula pitiayumi* ($\chi^2 = 12.86$, $df = 3$, $P < 0.01$) increased in relative abundance with decreases in area (Appendix).

The sum of relative abundances of species of trunk insectivores increased ($\chi^2 = 10.8$, $df = 1$, $P < 0.01$) from A (4.06) to G (5.24) as the result of a substantial increase in relative abundance of two species: *Cranioleuca obsoleta* (0.21 in A and 1.54 in G) and *C. pallida* (0.14 in A and 0.93 in G).

Relative abundances of *Furnarius rufus* ($\chi^2 = 49.89$, $df = 2$, $P < 0.001$), *Tyrannus melancholicus* ($\chi^2 = 23$, $df = 3$, $P < 0.001$), and *Phyllomyias fasciatus* ($\chi^2 = 39.72$, $df = 3$, $P < 0.001$) generalized insectivores, increased with decreases in area (Appendix). The sum of the relative abundances of this group was higher ($\chi^2 = 8.43$, $df = 1$, $P < 0.01$) in G (3.82) than A (2.93).

The sum of the relative abundances of frugivores decreased quickly ($\chi^2 = 176.93$, $df = 3$, $P < 0.001$) with decreases in area: A, 4.18; B, 2.89; C, 1.76, and G, 0.92. Only *Leptotila verreauxi* ($\chi^2 = 20.43$, $df = 3$, $P < 0.001$) and *L. rufaxilla* ($\chi^2 = 11.96$, $df = 3$, $P < 0.01$) increased in relative abundance.

DISCUSSION

Number of species.—Based on censuses from a few visits to many islands in the species/area studies, Haila and Järvinen (1981: 561) suggested that the “gain by increasing the number of visits to an island is the improved accuracy in the recording of rare spe-

cies.” Almost 90% of the species in a site are recorded during a single visit (Haila and Kuusela 1982). Taking into account the point counts of one year carried out in the present study, the combined samplings in A, B, C, and G from September to December (four visits) revealed 73–78% of the total species in these sites; this is less than the 90% predicted by Haila and Kuusela (1982). The fewer species we recorded in four visits is probably due to a higher proportion of rare species in our study sites. Therefore researchers in the Neotropical region, especially in forests, should make several visits to a site instead of a single visit.

There was a strong correlation ($r = 0.92$, $df = 10$, $P < 0.001$) between the number of bird species and the size of the forest patches in the Campos Gerais region. Other effects, such as habitat heterogeneity, might be more important than area in predicting the number of species found on an island (Martin et al. 1995). In more homogeneous sites it is expected that the effect of area would increase (Connor and McCoy 1979). Galli and co-workers (1976) studied woodlots in New Jersey with similar foliage height diversity and found a strong correlation between the number of species and size of the area. Martin (1981) studied homogeneous shelterbelts in South Dakota and concluded that area was the most important factor in determining the number of species. The similarity in vegetation structure between Campos Gerais forest patches is due to their being at approximately the same stage of ecological succession (Klein 1960, 1972; Klein and Hatschbach 1971; Maack 1981), and probably explains the high species/area correlation.

Based on the study by Tomialojc and co-workers (1984) in Poland, Blondel (1986) suggested that the habitats in large forests appear to be broken into a mosaic of “sink” and “source” because a large forest is represented by a mosaic of habitat patches. This results in a potential heterogeneity of the distribution of birds in large forests. In order to test the source/sink (Blondel 1986) role of larger forests, we calculated the β -diversity (Whittaker 1960) among the six points sampled monthly, in the 9 ha patch (G) and in the largest patch (A, 840 ha). The mean β -diversity was higher in A (1.68) than in G (1.27; Mann-Whitney

U-test: $U = 12.5$, $P < 0.05$), which suggests a more homogeneous bird distribution in the smaller area. The average number of species per point sampled was not significantly different (Tukey test: $P > 0.05$) between G and A, which suggests that the higher number of total species in the largest patch is mainly due to the heterogeneity of species' distributions compared to smaller patch.

It was expected that there would be more species in A (138 species, 840 ha) than in G (91 species, 9 ha) because of the difference in size of the fragments. The small difference can be explained by the heterogeneity of species distribution in A; the area sampled in A (24 sampled points, which represents around 80 ha) corresponds to about 10% of the total site, but the total area of G (9 ha) was sampled. Two hundred and seven species were recorded in A in a parallel study (Anjos 1992). Thus, the heterogeneity in bird distribution resulted in just 67% of the total avifauna in A being recorded in this study.

Composition of the bird communities.—In the Neotropics, as in the rest of the world, losses of species and changes in avian community composition occur with fragmentation of forest areas. In the Campos Gerais, the scarcity of forest species are, in part, balanced by gains in edge species (Fig. 3). Willis (1979) pointed out that the woodlots of São Paulo, southeastern Brazil, have become more like temperate zone forests with an emphasis on oscine birds characteristic of canopy and edge. Bierregaard and Lovejoy (1988) noted some edge species (*Troglodytes aedon* and *Ramphocelus carbo*) wandering into small forest patches (1 ha) after experimental deforestation in Amazonia. In the Campos Gerais region a gradual increase in the ratio of edge species to forest species was obvious with a decrease in fragment area. The majority of these edge species are oscines, some of them living in the canopy.

The proportion of forest/edge species does not seem to be related only to the size of the area. MacArthur and Wilson (1963, 1967) demonstrated that isolation is also an important factor. Among the isolated patches, L (1.5 ha) possessed a higher proportion of forest species than F (10 ha), H (8.5 ha), I (6.5 ha), or J (4 ha) probably because it was closer to the largest patch (Fig. 3, Table 1).

Among forest birds, the principal decrease in number of species in the Campos Gerais patches was associated with the loss of understory species. Canopy species probably fly to a nearby patch when there is a shortage of resources. Bierregaard and Lovejoy (1989) verified a decrease in the number of species also occurring among understory birds in Amazonia.

Aleixo and Vielliard (1995) pointed out that leaf insectivores of the understory were those most likely to be absent in a woodlot of 251 ha in São Paulo. We also found that most of the understory species that were absent from the small patches in the Campos Gerais region were leaf insectivores. Trunk insectivores were rarely found in small woodlots by Willis (1979); these were mostly small birds, such as *Picumnus* spp. (12 g) and *Veniliornis spilogaster* (43 g). Large trunk insectivores, such as *Phloeocastes robustus* (263 g) and *Dryocopus lineatus* (246 g), were recorded only in the forest of our study. Only small or mid-size species such as *Cranioleuca obsoleta* (14 g), *C. pallida* (12 g), *Lepidocolaptes squamatus* (28 g), and *Veniliornis spilogaster* were recorded in the smallest patches (Appendix).

Frugivores were rare in small patches of forest of Amazonia (Bierregaard and Lovejoy 1989) and São Paulo (Willis 1979, Aleixo and Vielliard 1995). Willis (1979) thought that because frugivores can easily travel to other woodlots to look for available resources they probably disappear from the small woodlots; they depend on scattered trees of different species at different seasons or years, and only large woodlots have enough tree diversity to support them. Frugivores occurred in all the patches we studied in the Campos Gerais region. This ability to easily move between patches may have prevented their numbers from declining (although the relative abundance of frugivores in smaller patches was low, as shown above).

Omnivores, which can switch from fruit to insects or vice versa, may benefit from small woodlots of São Paulo (Willis 1979). This group was represented by the greatest number of species in the Campos Gerais and tended to increase its contribution to the avifaunal composition with decreases in area; the sum of relative abundance increased from A (6.56) to G (9.0).

The present composition of the avifauna in the patches at the Campos Gerais region is the result of a long period during which, presumably, many factors have operated. Forest patches resulting from human disturbance of a continuous forest are isolated more rapidly. The effects of isolation on natural and artificial forest fragments may be different. According to Willis (1979), frugivores seem to be more sensitive to isolation in woodlots in São Paulo than in those of the Campos Gerais. But the woodlots studied by Willis (1979) are larger and more isolated than the patches studied in Campos Gerais. Thus, a study carried out under similar conditions is necessary for a more precise comparative analysis.

Relative abundance.—Vielliard and Silva (1990) and Aleixo and Vielliard (1995), using the same census method of point counts in São Paulo, Brazil, obtained a similar pattern of monthly variation in number of contacts as we did (Fig. 5). This is probably because September–December is the main period when all the species are more obvious when they breed and vocalize (Vielliard and Silva 1990, Aleixo and Vielliard 1995). There are also summer transients of some species in the study area from September to March (Anjos and Graf 1993). Therefore, counts of relative abundance are influenced by vocalization and migratory behavior. Because censuses were performed monthly in each patch, seasonal variation was assumed to be the same for all sites, making comparative analysis possible between the patches. In addition, because habitat physiognomy was similar for all of our patches, bias between the sites resulting from differences in detection of vocalizations (Schieck 1997) was unlikely.

Density compensation was detected in the present study for several species. For edge species the greater relative abundance is probably due to the relatively greater habitat area in the smaller patches. Edge species may also be better colonizers of isolated patches than forest species.

Decreased competition in smaller patches could explain density compensation (Ricklefs and Cox 1978). This seems to be the case for two leaf insectivores (*Thamnophilus caerulescens* and *Parula pitiayumi*) and some trunk insectivores (*Veniliornis spilogaster*, *Lepidocolaptes squamatus*, *Cranioleuca obsoleta*,

and *C. pallida*) in the present study. These groups decreased in number of species as area decreased, which could mean fewer competitors. However, documenting that competition occurs among species is not easy (Wiens 1989).

The “habitat appropriation” hypothesis of Blondel and coworkers (1988; a population size increases in an island because of an expansion of habitat occupation) was examined with two trunk and twig insectivores. *Cranioleuca obsoleta* ($\chi^2 = 162.72$, $df = 3$, $P < 0.05$) and *C. pallida* ($\chi^2 = 91.41$, $df = 3$, $P < 0.05$) increased in relative abundance with decreases in area (Appendix). Points were selected in A and G with either dense or open understory. The relative abundance of the two species was calculated in these two habitats (dense and open understory). *Cranioleuca obsoleta* had a relative abundance of 0.33 in open understory and 0.08 in dense understory areas of the 840 ha patch (A) but 2.07 and 1.06, respectively, in the 9 ha patch (G). *Cranioleuca pallida* was not observed in dense understory and had a relative abundance of 0.67 in open understory areas of A, and 0.43 and 1.29 respectively in G. This suggests that both species increase the habitats they use (they tended to be more abundant in areas of dense understory in G). These results were consistent with what could be interpreted as the “habitat appropriation” hypothesis. This should be considered as a complementary explanation for density compensation. *Cranioleuca obsoleta* also was common with high relative abundance in another natural patch of forest in Curitiba city, Paraná (Anjos and Laroca 1989).

The causes of density compensation are not clear but they may be different for each species.

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LITERATURE CITED

- ALEIXO, A. AND J. M. E. VIELLIARD. 1995. Composição e dinâmica da avifauna da mata de Santa Genebra, Campinas, São Paulo, Brasil. *Rev. Bras. Zool.* 12: 493–511.
- ANJOS, L. DOS. 1992. Riqueza e abundância de aves em “ilhas” de floresta de araucária. Ph.D. diss., Univ. Federal do Paraná, Curitiba, Brazil.
- ANJOS, L. DOS AND S. LAROCA. 1989. Abundância relativa e diversidade específica em duas comunidades urbanas de aves de Curitiba (sul do Brasil). *Arq. Biol. Tecnol. (Curitiba)* 32:637–643.
- ANJOS, L. DOS AND V. GRAF. 1993. Riqueza de aves da fazenda Santa Rita, região dos Campos Gerais, Palmeira, Paraná, Brasil. *Rev. Bras. Zool.* 10:673–693.
- ANJOS, L. DOS, K.-L. SCHUCHMANN, AND R. BERNDT. 1997. Avifaunal composition, species richness, and status in the Tibagi River basin, Paraná State, southern Brazil. *Ornitol. Neotrop.* 8:145–173.
- BELTON, W. 1984. Birds of Rio Grande do Sul, Brazil. Part 1. *Bull. Amer. Mus. Nat. Hist.* 178:369–636.
- BELTON, W. 1985. Birds of Rio Grande do Sul, Brazil. Part 2. *Bull. Amer. Mus. Nat. Hist.* 180:1–241.
- BIERREGAARD, R. O., JR. 1990. Avian communities in the understory of the Amazonian forest fragments. Pp. 333–343 in *Biogeography and ecology of forest bird communities* (A. Keast, Ed.). SPB Academic. The Hague, Netherlands.
- BIERREGAARD, R. O., JR. AND T. E. LOVEJOY. 1988. Birds in Amazonian forest fragments: effects of insularization. *Proc. Ornithol. Congr.* 19:1564–1579.
- BIERREGAARD, R. O., JR. AND T. E. LOVEJOY. 1989. Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonica* 19: 215–241.
- BLONDEL, J. 1986. *Biogéographie évolutive*. Masson, Paris, France.
- BLONDEL, J. 1991. Birds in biological isolates. Pp. 45–72 in *Bird population studies* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hiron, Eds.). Oxford Univ. Press, Oxford, U.K.
- BLONDEL, J., C. FERRY, AND B. FROCHOT. 1970. La méthode des indices ponctuels d’abondance (I.P.A.) ou des relevés d’avifaune par “stations d’écoute”. *Alauda* 38:55–71.
- BLONDEL, J., D. CHESSEL, AND B. FROCHOT. 1988. Birds impoverishment, niche expansion, and density inflation in mediterranean island habitats. *Ecology* 69:1899–1917.
- CONNOR, E. F. AND E. D. MCCOY. 1979. The statistics and biology of the species-area relationship. *Am. Nat.* 113:791–833.
- FITZPATRICK, J. W. 1980. Foraging behavior of Neotropical tyrant flycatchers. *Condor* 82:43–57.
- GALLI, A. E., C. F. LECK, AND R. T. FORMAN. 1976. Avian distribution patterns within sized forest islands in central New Jersey. *Auk* 93:356–365.
- HAILA, Y. AND O. JÄRVINEN. 1981. The underexploited potential of bird censuses in insular ecology. *Stud. Avian Biol.* 6:559–565.
- HAILA, Y. AND S. KUUSELA. 1982. Efficiency of one visit censuses of birds breeding on small islands. *Ornis Scand.* 13:17–24.
- KARR, J. R. 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. *Am. Nat.* 119: 220–239.
- KLEIN, R. M. 1960. O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12:17–44.
- KLEIN, R. M. 1972. As florestas da América do Sul. Univ. de Brasília, Brasília, Brazil.
- KLEIN, R. M. AND G. HATSCHBACK. 1971. Fitofisionomia e notas complementares sobre a mapa fitogeográfico de Quero-quero (Paraná). *Bol. Par. Geoc.* 28:159–188.
- LECK, C. F. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. *Auk* 96:343–352.
- MAACK, R. 1981. *Geografia física do Estado do Paraná*. Livraria José Olympio, Rio de Janeiro, Brazil.
- MACARTHUR, R. AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373–387.
- MACARTHUR, R. AND E. O. WILSON. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, New Jersey.
- MACARTHUR, R., J. R. KAAR, AND J. M. DIAMOND. 1972. Density compensation in island faunas. *Ecology* 53:330–342.
- MARTIN, J.-L., A. J. GASTON, AND S. HITIER. 1995. The effect of island size and isolation and old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). *Oikos* 72:115–131.
- MARTIN, T. E. 1981. Limitation in small habitat islands: chance or competition. *Auk* 98:715–734.
- MEYER DE SCHAUENSEE, R. 1982. *A guide to the birds of South America*. Academy Natural Science, Philadelphia, Pennsylvania.
- PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43:185–215.
- RICKLEFS, R. E. AND G. W. COX. 1978. Stage of taxon cycle, habitat distribution and population density in the avifauna of the West Indies. *Am. Nat.* 112: 875–895.
- RIDGELY, R. S. AND G. TUDOR. 1989. *The birds of South America*. Vol. 1. Oxford Univ. Press, Oxford, U.K.
- RIDGELY, R. S. AND G. TUDOR. 1994. *The birds of South America*. Vol. 2. Oxford Univ. Press, Oxford, U.K.
- SAS INSTITUTE, INC. 1989. *SAS/STAT® user’s guide*, version 6.11, fourth ed. SAS Institute, Inc., Cary, North Carolina.

- SCHIECK, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. *Condor* 99:179–190.
- SICK, H. 1997. *Ornitologia brasileira*. Nova Fronteira ed., Rio de Janeiro, Brazil.
- TOMIALOJC, L., T. WESOLOWSKI, AND W. WALANKIEWICZ. 1984. Breeding bird community of a primeval temperate forest (Bialowieza National Park, Poland). *Acta Ornitol.* 20:241–310.
- VIELLIARD, J. E. M. AND W. R. SILVA. 1990. Nova metodologia de levantamento quantitativo da avifauna e primeiros resultados no interior do Estado de São Paulo, Brasil. Pp. 117–151 in *Anais do IV Encontro de Anilhadores de Aves* (S. Mendes, Ed.). Univ. Federal Rural de Pernambuco Press, Recife, Brazil.
- WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30:279–338.
- WIENS, J. A. 1989. *The ecology of bird communities*. Vol. 2. Cambridge Univ. Press, Cambridge, U.K.
- WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44:153–169.
- WILLIS, E. O. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. *Papéis Avulsos Zoologia* 33:1–25.
- WRIGHT, S. J. 1980. Density compensation in island avifaunas. *Oecologia* 45:385–389.

APPENDIX. Relative abundance of the bird species in the sites A, B, C, and G; (s) indicates significant difference (χ^2 , $P < 0.05$) between the number of contacts when it is recorded in at least 3 sites and (*) indicates the first 12 species with highest values of relative abundance in each site. Only the occurrence (1) is indicated for other sites.

Family Species	Sites												^a Habitat	^b Habitat			
	A	B	C	G	D	E	F	H	I	J	L	M					
TINAMIDAE																	
<i>Crypturellus obsoletus</i> (s)	0.472	0.113	0.028												FU	OM	OM
ARDEIDAE																	
<i>Syrigma sibilatrix</i>		0.097	0.153	0.194	1	1		1		1					OA	OM	OM
THRESKIORNITHIDAE																	
<i>Theristicus caudatus</i>	0.361	0.306	0.403	0.278		1		1							OA	OM	OM
CATHARTIDAE																	
<i>Coragyps atratus</i>	0.014		0.042	0.042	1	1		1		1					OA	CA	CA
<i>Cathartes aura</i>					1	1		1							OA	CA	CA
ACCIPITRIDAE																	
<i>Buteo albicaudatus</i>				0.028											OA	CA	CA
<i>Buteo uagirostris</i> (s)	0.042	0.081	0.056	0.222	1	1		1		1				ED	CA	CA	CA
<i>Heterospizias meridionalis</i>				0.083										OA	CA	CA	CA
FALCONIDAE																	
<i>Herpetotheres cachimans</i>		0.016													FC	CA	CA
<i>Micrastur ruficollis</i>	0.111														FC	CA	CA
<i>Milvago chiuuachina</i>		0.016	0.097	0.056	1	1		1		1					ED	OM	OM
<i>Polyborus plancus</i> (s)	0.083	0.032	0.153	0.138	1	1		1		1					ED	OM	OM
<i>Falco femoralis</i>															OA	CA	CA
<i>Falco sparverius</i>										1					OA	GI	GI
CRACIDAE																	
<i>Peuelope obscura</i> (s)	0.014	0.032	0.069	0.125	1	1		1		1					FM	OM	OM
PHASIANIDAE																	
<i>Odontoptorus capueira</i> (s)	0.125	0.048	0.014												FU	OM	OM
RALLIDAE																	
<i>Aramides saracura</i>	0.028	0.048			1										FU	OM	OM

APPENDIX. CONTINUED.

Family Species	Sites													^a Habitat	^b Habitat	
	A	B	C	G	D	E	F	H	I	J	L	M				
FURNARIIDAE																
<i>Clibanornis dendrocolaptooides</i>	0.028			0.014	1									1	FU	GI
<i>Furnarius rufus</i> (s)		0.032	0.611*	0.819*	1	1	1	1	1	1					ED	GI
<i>Leptasthenura striolata</i> (s)	0.042	0.016	0.139	0.097											FC	LI
<i>Leptasthenura setaria</i> (s)	0.680*	0.048	0.847*	0.264	1	1	1	1	1						FC	LI
<i>Synallaxis ruficapilla</i>	0.139	0.081			1										FU	LI
<i>Synallaxis spixi</i>			0.042	0.042	1										FU	LI
<i>Synallaxis cinerascens</i> (s)	0.333	0.419*	0.181	0.014						1					FU	LI
<i>Cranioleuca obsoleta</i> (s)	0.208	0.081	0.528	1.542*	1	1	1	1	1	1	1				FM	TI
<i>Cranioleuca pallida</i> (s)	0.139	0.032	0.444	0.931*						1					FM	TI
<i>Anumbius annumbi</i>			0.236	0.278	1	1	1	1	1	1					ED	GI
<i>Syndactyla rufosuperciliata</i> (s)	0.431	0.258	0.417	0.167	1	1	1	1	1	1	1				FM	LI
<i>Anabacerthia anaurois</i>	0.153	0.065	0.042	0.056											FM	LI
<i>Philydor rufus</i> (s)	0.375	0.145	0.125												FC	LI
<i>Heliobletus contaminatus</i>	0.208	0.145	0.222		1	1									FM	TI
<i>Xenops rutilans</i>	0.083	0.032	0.028												FM	TI
<i>Xenops minutus</i>	0.069	0.032													FM	LI
<i>Sclerurus scansor</i>	0.194	0.016													FU	GI
<i>Lochinias nematura</i>	0.167	0.048			1					1					FU	GI
FORMICARIIDAE																
<i>Batara cinerea</i>	0.055														FU	OM
<i>Mackenziaena leachii</i>	0.014	0.016													FU	OM
<i>Biatas nigropectus</i>	0.028														FM	LI
<i>Thamnophilus caerulescens</i> (s)	0.402	0.371	0.667*	0.403	1	1	1	1	1	1	1				FM	LI
<i>Dysithamnus mentalis</i> (s)	0.375	0.274	0.042	0.083											FM	LI
<i>Drymophila malura</i>	0.181	0.161													FU	LI
<i>Pyriglena leucoptera</i>	0.111	0.032													FU	LI
<i>Chamaeza campanisona</i>	0.764*	0.177													FU	OM
<i>Chamaeza ruficauda</i>	0.653*	0.161													FU	OM
<i>Hylopezus nattereri</i>	0.139	0.048													FU	GI
<i>Conopliaga lineata</i>	0.333	0.323		0.194	1	1	1	1	1	1	1				FU	GI

APPENDIX. CONTINUED.

Family Species	Sites													^a Habitat	^b Habit	
	A	B	C	G	D	E	F	H	I	J	L	M				
<i>Tolmomyias sulphureus</i>	0.292	0.065			1	1								FC	LI	
<i>Todirostrum plumbeiceps</i>	0.014					1	1							FU	LI	
<i>Idioptilon nidipendulum</i>	0.028													FU	LI	
<i>Myiornis auricularis</i>	0.014	0.032												FU	LI	
<i>Hemitriccus obsoletus</i>	0.167	0.048												FU	LI	
<i>Pogonotriccus eximius</i> (s)	0.333	0.161	0.042	0.194		1	1	1	1	1	1			FM	LI	
<i>Phylloscartes ventralis</i> (s)	0.431	0.290	0.694*	0.542	1	1	1	1	1	1	1			ED	LI	
<i>Phylloscartes oustaleti</i>	0.097													FM	LI	
<i>Serpophaga subcristata</i> (s)	0.014		0.056	0.236	1	1	1	1	1	1	1			ED	LI	
<i>Elaenia parvirostris</i>			0.056	0.097	1	1	1	1	1	1	1			ED	OM	
<i>Elaenia mesoleuca</i> (s)	0.042	0.065	0.264	0.292	1	1	1	1	1	1	1			ED	OM	
<i>Elaenia chiriquensis</i>			0.014	0.014										ED	OM	
<i>Elaenia obscura</i>		0.032	0.069	0.028	1	1	1	1	1	1	1			ED	OM	
<i>Myiopagis caniceps</i>	0.056													FC	LI	
<i>Camptostoma obsoletum</i>	0.153	0.113	0.222	0.250	1	1	1	1	1	1	1			FC	GI	
<i>Phyllomyias fasciatus</i> (s)	0.014	0.016	0.292	0.333										FC	GI	
<i>Acrochordopus burmeisteri</i>	0.042		0.069											FM	LI	
<i>Leptopogon amaurocephalus</i>	0.111													FU	LI	
<i>Pipromorpha rufiventris</i>	0.167	0.016				1								FU	FR	
CORVIDAE																
<i>Cyanocorax caeruleus</i> (s)	0.403	0.194	0.208	0.556	1	1	1	1	1	1	1			FC	OM	
<i>Cyanocorax chrysops</i>			0.014						1	1	1			FM	OM	
TROGLODYTIDAE																
<i>Troglodytes aedon</i>			0.083	0.167	1	1	1	1	1	1	1			ED	LI	
TURDIDAE																
<i>Platycichla flavipes</i>		0.048						1	1	1	1			FM	OM	
<i>Turdus nigriceps</i>			0.014	0.097	1	1	1	1	1	1	1			FM	OM	
<i>Turdus rufiventris</i> (s)	0.611*	0.887*	0.847*	1.042*	1	1	1	1	1	1	1			FM	OM	
<i>Turdus amaurochalinus</i> (s)	0.014	0.113	0.194	0.319	1	1	1	1	1	1	1			FM	OM	
<i>Turdus albicollis</i>	0.486	0.354	0.264	0.486	1	1	1	1	1	1	1			FU	OM	

APPENDIX. CONTINUED.

Family Species	Sites													aHabitat	bHabit	
	A	B	C	G	D	E	F	H	I	J	L	M				
FRINGILLIDAE																
<i>Saltator similis</i> (s)	0.278	0.258	0.250	0.472	1	1	1	1	1	1	1	1	1	1	ED	OM
<i>Pitylus fuliginosus</i>	0.042									1					FM	OM
<i>Volatinia jacarina</i>															ED	OM
<i>Tiaris fuliginosa</i>	0.028														FU	OM
<i>Sporophila caeruleescens</i>			0.028		1			1	1				1		ED	OM
<i>Sicalis flaveola</i>			0.042	0.014						1			1		ED	OM
<i>Haplopiza unicolor</i> (s)	0.347	0.419*		0.056											FU	OM
<i>Zonotrichia capensis</i> (s)	0.070	0.210		0.481	1			1	1	1	1		1		ED	OM
<i>Poospiza lateralis</i> (s)	0.014		0.208	0.389	1			1	1	1	1		1		ED	OM
<i>Carduelis magellanicus</i> (s)	0.014	0.032	0.028	0.139	1			1	1	1	1		1		ED	OM

^a Habitat (OA = open area; ED = edge; FU = forest understory; FM = forest mid-levels; FC = forest canopy)

^b Feeding habit (OM = omnivore; FR = frugivore; NE = nectarivore; CA = carnivore; GI = generalized insectivore; LJ = leaf insectivore; TI = trunk insectivore) is shown for each species.